

**A NEW SPECIES OF *PLEUROTHALLIS* (ORCHIDACEAE:
PLEUROTHALLIDINAE) FROM VALLE DEL CAUCA, COLOMBIA
AND A NOTE ON THE RELATIONSHIP BETWEEN SUBSECTIONS
MACROPHYLLAE-RACEMOSAE AND *ANTENNIFERAE***

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ABSTRACT. A new species of *Pleurothallis* from subsection *Macrophyllae-Racemosae* is described from Valle del Cauca, Colombia. Morphological characteristics to distinguish this species from *Pleurothallis bicornis*, *P. subreniformis* and *P. torrana* are presented. The micromorphology of the lip of the new species was studied utilizing scanning electron microscopy. Labellar micromorphology is discussed in relation to putative pollination mechanisms.

KEY WORDS: *Antenniferae*, glenion, labellum, *Macrophyllae-Racemosae*, *Pleurothallis*, pollination

Introduction. *Pleurothallis* section *Macrophyllae-Racemosae* was created by Lindley (1859). Luer (1988) demoted the section to subsection *Macrophyllae-Racemosae*, joining *Pleurothallis* subsections *Acroniae*, *Antenniferae*, *Longiracemosae* and *Macrophyllae-Fasciculatae*. Luer (1999) in *Icones Pleurothallidarum XVIII* recognized 37 species in the subsection with the type being *Pleurothallis lindenii* Lindl. Since that monograph on the subsection only *Pleurothallis papilingua* A.Doucette & J.Portilla has been described. At this time, the group can be considered to contain between 38 and 50 species, depending on synonymy. However, Luer (1999) acknowledged that “*All the subsections are interrelated, sometimes with overlapping boundaries and intermediate species*”. In particular, there seems to be a high degree of morphological overlap between subsections *Macrophyllae-Racemosae* and *Antenniferae*. Indeed, there is no single morphological character or group of characters that can reliably place a

species in subsection *Macrophyllae-Racemosae* versus *Antenniferae*.

Unfortunately, the molecular phylogenetic study of the Pleurothallidinae by Pridgeon, Solano and Chase (2001) did not include representatives of either subsection and, therefore, provided no information on whether the two groups should be merged into a single taxonomic unit. The ongoing phylogenetic studies of *Pleurothallis* by Wilson *et al.* (2011, 2013) and Wilson (unpubl. data) utilizing nuclear internal transcribed spacer (nrITS) and plastid *matK* sequences, incorporating representatives of both subsections, indicate that while there is a strongly-supported clade for subgenus *Pleurothallis* (at least if subsection *Macrophyllae-Fasciculatae* is excluded), there is only weak support for groupings below the level of subgenus. In other words, preliminary phylogenetic data do not support a distinction between subsections *Macrophyllae-Racemosae* and *Antenniferae*.

Considering this and the lack of a discriminatory morphological character, the two subsections might be considered a single group. Since subsection *Antenniferae* contains 38 to 49 species, depending on synonymy (Luer 1999), the two subsections together would include somewhere between 76 and 99 species.

If we consider the two subsections as a single group, the species are distributed from Central America (*Pleurothallis colossus* Kraenzl. ex Kerch. and *Pleurothallis crescentilabia* Ames) through the Andean countries of Venezuela, Colombia, Ecuador and Peru, as far south as Bolivia (*Pleurothallis antennifera* Lindl., *Pleurothallis demissa* Luer & R.Vásquez, *Pleurothallis lamellaris* Lindl. and *Pleurothallis saltatoria* Lindl.); one species occurs in Guyana and Suriname (*Pleurothallis suspensa* Luer); and one species occurs in the Caribbean (*Pleurothallis revoluta* (Ruiz & Pav.) Garay) (Luer 1999). Based on the number of collected species, Ecuador would appear to be the center of diversity for this group, however, there is probably a collection bias, since, until recently, Colombia was less accessible than Ecuador.

The species of *Pleurothallis* in the *Macrophyllae-Racemosae/Antenniferae* group are frequently misidentified. For example, *P. lindenii* and *Pleurothallis secunda* Poepp. & Endl. have been repeatedly confused (Luer 1999). In part this is because, aside from a few very easily identifiable species such as *P. colossus* and *P. hemisphaerica* Luer & R.Escobar, identification relies heavily upon the morphology of the labellum or “lip” and in particular the presence or absence of calli, which usually requires dissection of the flower. Such is the case in distinguishing the almost identical *Pleurothallis magnifica* Luer & R.Escobar and *Pleurothallis orthostachys* Luer & R.Escobar. Indeed, because of the morphological similarity of the species in the *Macrophyllae-Racemosae/Antenniferae* group, confusion among the described species and scant attention paid to the group, there may well be many more than the estimated 76–99 species for the two combined subsections. In this paper we describe the first of a series of new species in the *Macrophyllae-Racemosae/Antenniferae* group.

Relatively little is known about pollination of species of *Pleurothallis sensu* Pridgeon, Cribb, Chase & Rasmussen (2005), but the genus is presumed to be pollinated predominantly by Diptera. Pollination

in the *Macrophyllae-Racemosae/Antenniferae* group has been studied more than any other group within the genus. Duque (1993) reported *Pleurothallis lindenii* (as *Pleurothallis secunda*) was pollinated primarily by Diptera while *Pleurothallis aves-seriales* Luer & R.Escobar (possibly *Pleurothallis antennifera*) was pollinated by Diptera and Hymenoptera. Calderón-Sáenz (2011) observed pollination of *Pleurothallis colossus* by Anthomyiid flies. Although unable to perform *in situ* pollination studies on the new species, in this paper we present data on lip morphology from macro-photography and scanning electron microscopy (SEM) and discuss labellar morphology in relation to putative pollination mechanisms.

Materials and Methods

Plant material— Plant material of the new species described in this article was examined *in situ* in Valle del Cauca, Colombia. Plant material was also examined in the collections of: Orquídeas del Valle, Cali, Colombia, where the plant was grown as *P. bicornis*; Carlos Mesa Londoño, Medellín, Colombia; Libia Orquídeas, Medellín, Colombia; and Ecuagenera, Gualaceo, Ecuador, where the plant was grown as *P. torrana*. Plants were imported into U.S.A from Ecuagenera as *P. torrana*, without collection data, and grown in cultivation by Wilson in Colorado and Pinnix in California. Material from these latter plants was used for the creation of the Lankester composite digital plate (LCDP) of the new species and for creation of herbarium specimens accessioned into the herbarium at Colorado College (COCO). Flowers of the studied species were preserved in Kew Mix (5% formalin [37.6% formaldehyde], 53% methanol, 5% glycerol, 37% deionized water).

Taxonomic comparisons— In order to determine novelty of the species described herein, plant material was first compared to species with which this plant had previously been confused, including *P. bicornis* and *P. torrana*, as well as with the similar species, *Pleurothallis subreniformis* Schltr. (Luer 1999). The putative new species was compared to descriptions of Colombian and Ecuadorian species from all pertinent literature: Dodson (2003), Dodson and Dodson (1980, 1982), Escobar (1994, 2006), Luer (1974, 1975a, 1975b, 1976, 1977, 1986, 1988, 2005, 2009, 2011) and Luer and Thorerle (2013).

Labellar micro-morphology—. Flowers were prepared for and examined by SEM using methods described previously (Wilson *et al.* 2016).

Results

Initial observations—. The new species was initially noticed by the first author in October 2009 among photos from the collection of Lynn O’Shaughnessy on the website of the Pleurothallid Alliance, listed as *Pleurothallis* sp. (O’Shaughnessy 04008) from Colombia. The species (Fig. 1) was subsequently observed by the first author in the collections of Ecuagenera, as *P. torrana*, and Orquideas del Valle, as *P. bicornis*. Preliminary comparison of the species to the drawings and descriptions of similar species (Fig. 2, Luer 1999) suggested that this plant was not *P. bicornis*, *P. torrana*, or the somewhat similar *P. subreniformis*.

Taxonomic comparisons—. Dimensions of the plant and flowers of the new species were compared to those of *P. bicornis* (Figs. 2A, 3), *P. subreniformis* (Figs. 2B, 4) and *P. torrana* (Fig. 2C) (Table 1). Particular emphasis was applied to a comparison of the lip of the putative new species with those of the described species (Fig. 5). Morphological comparisons of *Pleurothallis caucensis* sp. nov. to the three aforementioned species, and to the other species in *Pleurothallis* subsections *Macrophyllae-Racemosae* and *Antenniferiae*, indicated that this was indeed a previously undescribed species.



FIGURE 1. *Pleurothallis caucensis* (yellow form). Photograph by William Pinnix from paratype M. Wilson, W. Pinnix & J. Portilla PL0976.

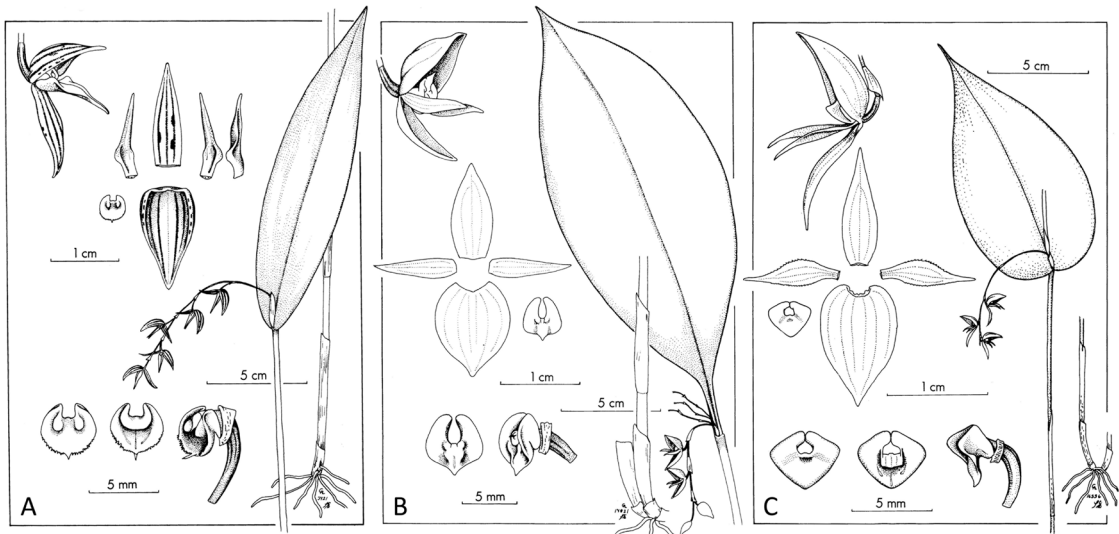


FIGURE 2. Drawings of A - *Pleurothallis bicornis*; B - *Pleurothallis subreniformis*; and C - *Pleurothallis torrana* (from Luer 1999, courtesy of Missouri Botanical Garden Press).



FIGURE 3. *Pleurothallis bicornis*. A – Raceme; B - Flower detail. Photographs by Lourens Grobler.

Geographic distribution of morphologically similar Macrophyllae-Racemosae/Antenniferae— The new species was photographed *in situ* (Fig. 6) on the eastern side of the Cordillera Occidental, near Calima Lake, in the Department of Valle del Cauca, Colombia (Fig. 7) in December 2015 by Haelterman. To our knowledge it has not been photographed *in situ* or collected from the wild in Ecuador where it appears to only occur in a commercial collection. *Pleurothallis torrana* is believed to be endemic to Cerro Torrá, on the western or Pacific side of the Cordillera Occidental, near Sipí, in the Department of Chocó, Colombia (Fig. 7) (Luer 1999). The similar species *P. bicornis* (Fig. 8) and *P. subreniformis* (Fig. 9) have both been photographed by Kay in the forests of NW Ecuador, but their occurrence in adjacent areas of Colombia has not been confirmed.

Labellar micromorphology— The lips of *P. caucensis*, *P. bicornis* and *P. subreniformis* each exhibit longitudinally-oriented calli on the central lobe of the lip. In *P. caucensis* the calli are poorly-

developed and lunate in top-view (Figs. 10–11). They flank a channel in front of the anther and an indistinct, small glenion immediately below the viscidium. In *P. bicornis* the calli are large and triangular in side-view, short and partially lunate in top view (Figs. 3B, 5A). In *P. subreniformis* the calli are low and rounded in side-view and long, lunate in top-view (Figs. 4B, 5B). Interestingly, the lip of *P. caucensis* exhibited liquid droplets, possibly nectar, on the anterior margin of the central lobe (Fig. 10). When examined by SEM from the anterior edge of the central lobe of the lip towards the anther, the relief of the lunate calli and the channel created between them was more apparent (Fig. 11). This channel bore the dehydrated remains of liquid, represented only by a thin, desiccated film.

Taxonomy

Pleurothallis caucensis Mark Wilson, *sp. nov.* (Figs. 1, 6, 10, 11, 12, 13)

TYPE: Colombia. Flowered in cultivation as *P.*



FIGURE 4. *Pleurothallis subreniformis*. A – Raceme; B - Flower detail. Photographs by Wilson (A) and Andreas Kay (B).

TABLE 1. Comparison of morphology and dimensions of *Pleurothallis caucensis* (this study, derived from all available material) with *Pleurothallis bicornis*, *Pleurothallis subreniformis* and *Pleurothallis torrana* (data from Luer 1999).

Plant part	<i>P. caucensis</i>	<i>P. bicornis</i>	<i>P. subreniformis</i>	<i>P. torrana</i>
Ramicaul length (cm)	45-75	35-75	40-92	17-35
Leaf size (cm)	11-28 × 4.5-11.2	15-22 × 4-9.5	25-31 × 8-14	13-14 × 6.5-7
Raceme length (cm)	11.5-16.3	10-18	5-8	~ 8
Dorsal sepal (mm)	14-15 × 12-13	13-17 × 3.5-6	12 × 4.5-5.5	12 × 3.75
Synsepal (mm)	16-18 × 8-10	13-17 × 14-16	11-12 × 8-9	12 × 8
Petals (mm)	15-19 × 5-6	12-16 × 2.75-3.5	10 × 2	9.5 × 2.5
Lip (mm)	5-6 × 5-6	3.5-4 × 4-5	3 × 4.5-5	2.25-4.25
Lip shape	suborbicular	suborbicular	hippocrepiform	subrhombic
Lip callus/calli	low calli in front of anther	large calli in front of anther	low rounded calli	small transverse callus
Fimbriae	short fimbriae all around lip	long fimbriae at apex only	no fimbriae	no fimbriae

bicornis by Carlos Augusto Mesa Londoño in Envigado, Colombia, Jan 27, 2017, M. Wilson & C. A. Mesa Londoño PL0993 (holotype: JAUM!).

Diagnosis. *Pleurothallis caucensis* can be distinguished from *P. bicornis* by the petals, which in *P. caucensis* are free, projected laterally and downward and in *P. bicornis* are adpressed and project forwards; by the lip which is completely fimbriated in *P. caucensis* and only fimbriated on the margin of the central lobe in *P. bicornis*; and by the lateral lobes of the lip which are flattened and surpass the column in *P. caucensis* and which are auriculate, not surpassing the column in *P. bicornis*. *Pleurothallis caucensis* differs from *P. subreniformis* in the length of the raceme, sepals and petals, which are longer in *P. caucensis* than in *P. subreniformis* (Table 1); and in the lip shape, which is suborbicular in *P. caucensis* and hippocrepiform with an acute apex on the midlobe in *P. subreniformis*. *Pleurothallis caucensis* differs from *P. torrana* in the length of the ramicauls, raceme, sepals and petals, all of which are longer in *P. caucensis* than in *P. torrana* (Table 1); in the lip shape which is suborbicular in *P. caucensis* and rhombiform in *P. torrana*; and in the

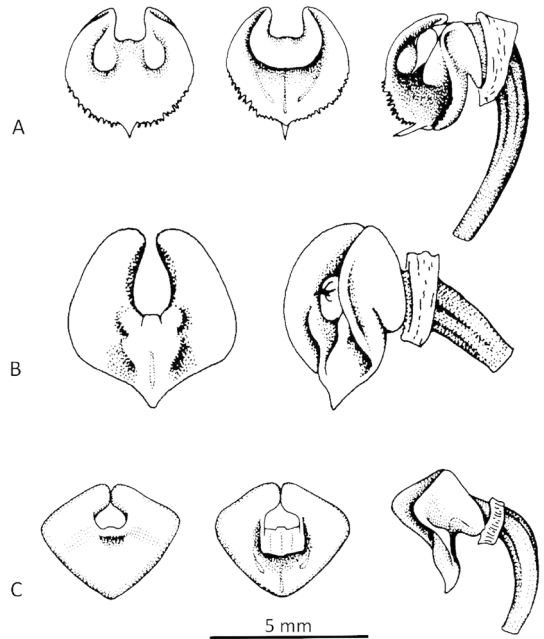


FIGURE 5. Drawings of lips of A - *Pleurothallis bicornis*; B - *Pleurothallis subreniformis*; and C - *Pleurothallis torrana*. Drawings from Luer 1999, courtesy of Missouri Botanical Garden Press..



FIGURE 6. *Pleurothallis caucensis* (orange form) *in situ* in Valle del Cauca, Colombia: A - Whole inflorescence; B - Flower front view. Photographs by David Haelterman.



FIGURE 7. Topographical map of Colombia indicating only known locality of *Pleurothallis caucensis* (black) and type locality of *Pleurothallis torrana* (white). Map courtesy of Freeworldmaps.net.



FIGURE 8. *Pleurothallis bicornis* in situ in NW Ecuador. A - Plant with inflorescences; B - Detail of inflorescences. Photographs by Andreas Kay.



FIGURE 9. *Pleurothallis subreniformis* in situ in NW Ecuador. A - Plant with inflorescences; B -Detail of inflorescences. Photographs by Andreas Kay.



FIGURE 10. Lip and column of *Pleurothallis caucensis*. A - Basal lobes of lip; B - Fimbriate margin of central lobe of lip; C - Lunate calli; D - Glenion below viscidium; E - Nectar-like liquid on central lobe of lip. Photograph by Carlos Mesa from *M. Wilson & C. A. Mesa Londoño PL0993*

lip callus, which consists of a pair of lunate calli in *P. caucensis* and a single transverse callus in *P. torrana*.

Plant large, terrestrial, caespitose, ~79–94 cm tall. *Roots* fibrous, coarse. *Ramical* spreading, terete, 45–75 cm, with basal sheath 4.55–7.20 cm long and mid-sheath, 7.3–9.2 cm long. *Leaves* sub-erect, becoming pendent,

ovate, acuminate, cuneate, 11–28 × 4.5–11.2 cm, entire. *Inflorescence* 1 pendent raceme per leaf, 3–8 flowers per raceme, 11.5–16.3 cm long, from reclining spathaceous bract 1.8–2.6 cm long, floral bract infundibular, 6–8 mm long. *Pedicel* 4.0–5.6 mm long. *Ovary* 7.0–10 mm long. *Flowers* non-resupinate in presentation, 2–3 × 1.6–1.8 cm. *Dorsal sepal* yellow lightly suffused with red-brown to darker orange-brown increasing in density toward apex, ovate, acute-acuminate, 14–15 × 12–13 mm, entire, glabrous, 3-veined. *Synsepal* yellow lightly suffused with red-brown to darker orange-brown increasing in density toward apex, ovate, concave, acute-acuminate, 16–18 × 8–10 mm, entire, glabrous, 6-veined. *Petals* yellow lightly suffused with red-brown increasing in density toward apex, lanceolate, acuminate, cuneate-humerate at base, 15–19 × 5–6 mm, entire, glabrous, 3-veined. *Lip* yellow, tri-lobed, infused with red-brown along margin of central lobe, suborbicular, 5–6 mm diameter, fimbriate, lateral lobes rounded, flanking the column, central lobe with two poorly-developed rounded lunate calli on central lobe in front of anther, small glenion below anther. *Column* yellow, stout, short, 2.8–3.1 × 0.8–1.0 mm, tightly fused to lip, anther apical, anther cap yellow.

ADDITIONAL MATERIAL STUDIED: Colombia. Flowered in cultivation as *P. bicornis* by Diana Garcia Lopera in Medellín, Colombia, Jan 27, 2017, *M. Wilson & D.*

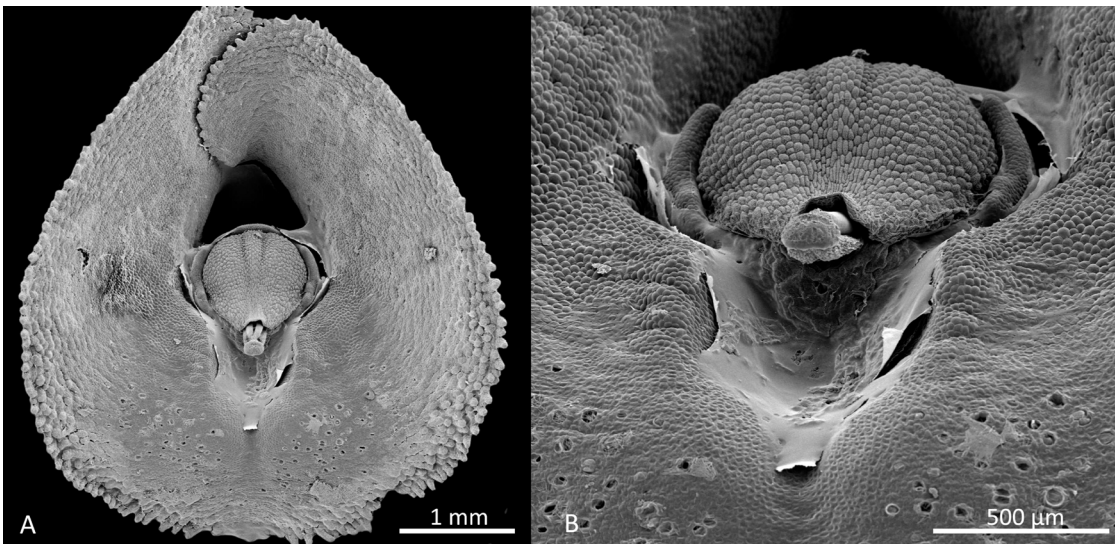


FIGURE 11. Scanning electron micrographs of *Pleurothallis caucensis*: A - Lip and anther; B - Detail of anther, viscidium and lip with calli. Micrographs by Katharine Dupree prepared from the paratype *M. Wilson & J. Portilla PL0756*.

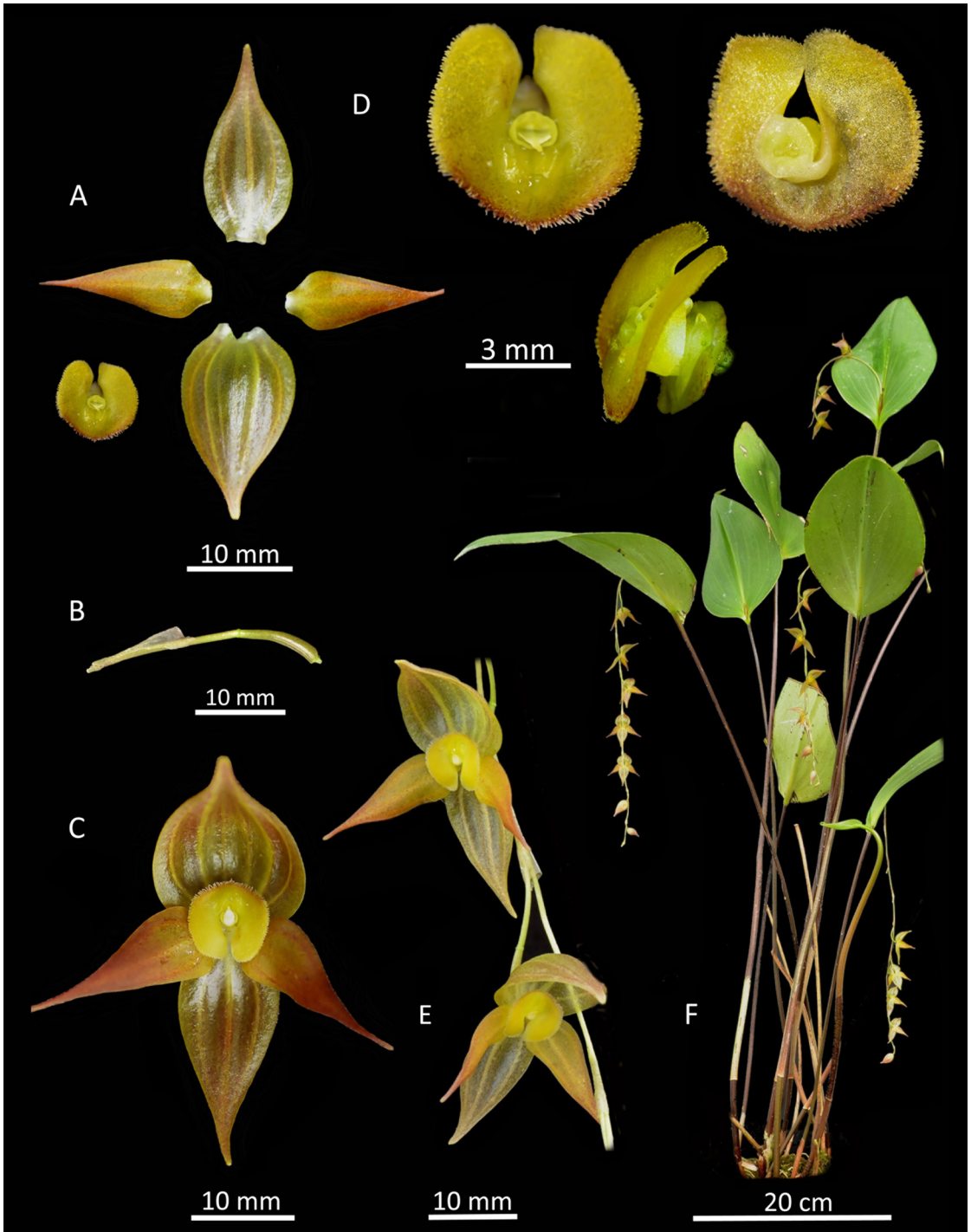


FIGURE 12. Lankester composite digital plate of *Pleurothallis caucensis*: A - Floral dissection; B - Pedicel, floral bract and ovary; C - Whole flower; D - Lip (front, rear and side); E - Partial raceme with flowers in non-resupinate orientation; F - Whole plant with inflorescences. LCDP prepared by Mark Wilson from the paratype *M. Wilson, W. Pinnix & J. Portilla PL0976*

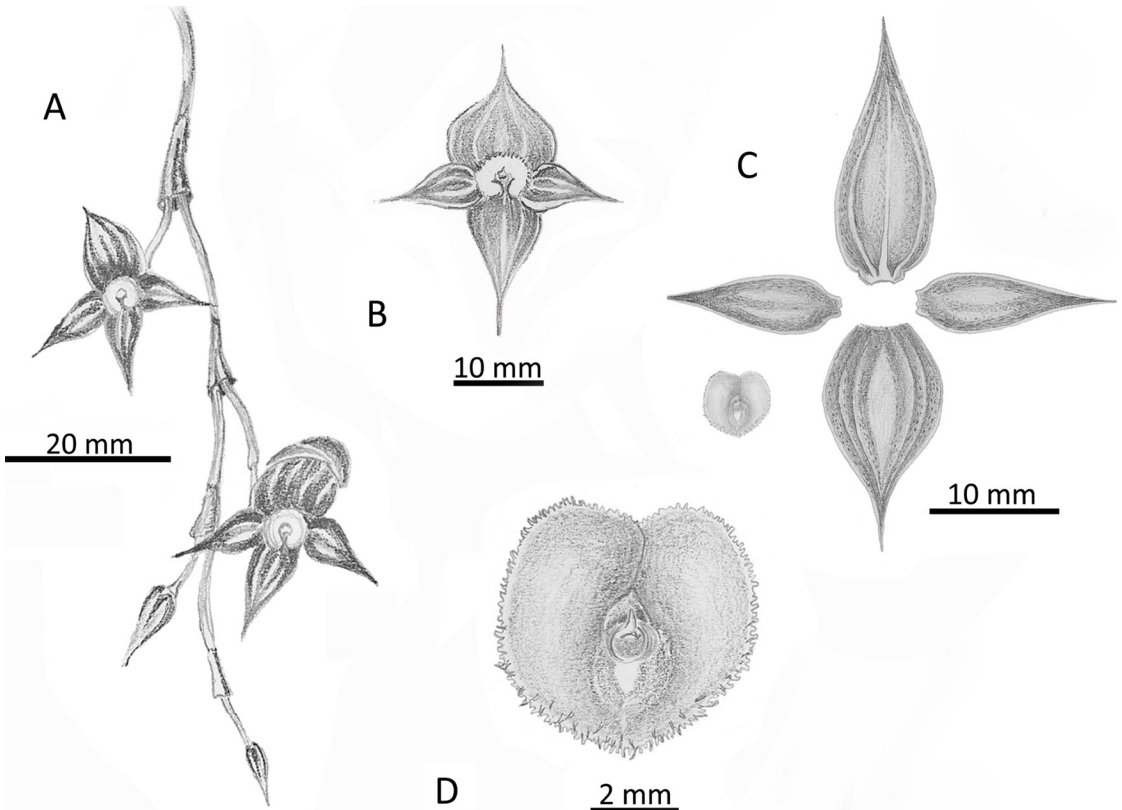


FIGURE 13. Drawing of *Pleurothallis caucensis*: A - Inflorescence; B - Whole flower; C - Floral dissection; D - Lip. Drawn by Jon Werner from the paratype *M. Wilson, W. Pinnix & J. Portilla PL0976*.

García Lopera PL0994 (paratype: JAUM!). Flowered in cultivation as *P. bicornis* by Andrea Niessen in Cali, Colombia, *M. Wilson & A. Niessen PL0995* (paratype: CUVC!). Ecuador. Purchased from Ecuagenera as *P. torrana*, without collection data, and flowered in cultivation in Colorado *M. Wilson & J. Portilla PL0756* (paratype: COCO!). Purchased from Ecuagenera as *P. torrana*, without collection data, and flowered in cultivation in California *M. Wilson, W. Pinnix & J. Portilla PL0976* (paratype: COCO!).

ETYMOLOGY: Named in reference to the only known locality of the species in Valle del Cauca, Colombia.

DISTRIBUTION AND HABITAT: *Pleurothallis caucensis* was observed growing terrestrially among dead leaves at an altitude of ~1800 m in the vicinity of montane forest near Calima Lake, Department of Valle del Cauca, Colombia. Other orchids in the vicinity included *Masdevallia caesia* and *Houlletia odoratissima*. To date, *P. caucensis* has not been observed in

neighboring Ecuador, despite occurring in collections in that country. It is possible, however, that it occurs in forests of northern Ecuador, in which case, collections from that region may exist in herbaria misidentified as *P. bicornis*, *P. subreniformis* or *P. torrana*. Until the presence of *P. caucensis* in Ecuador can be verified, it should not be added to the flora of that country.

CONSERVATION STATUS: The location in which *P. caucensis* was observed growing naturally is not in a protected area and cannot be considered secure. Although *P. caucensis* occurs in collections in Colombia, Ecuador, U.S.A and England, the level of genetic variation among these plants is unknown, so the value of these collections for *ex situ* conservation cannot be assessed.

Pleurothallis subsection *Macrophyllae-Racemosae* is the third most species-rich group in subgenus *Pleurothallis* after subsections *Macrophyllae-Fasciculatae* and *Acroniae*; or if we

consider subsections *Macrophyllae-Racemosae* and *Antenniferae* to represent a single taxonomic group, then the combined subsection rises to second most species-rich. The description of *P. caucensis* brings the total in the combined group to 77–100 species, depending on synonymy. However, there are probably many more species in the group to be described, since the group has received less attention than others within *Pleurothallis sensu* Pridgeon *et al.* (2005), this being only the second new species since the monograph by Luer (1999).

While *P. caucensis* is superficially similar to *P. bicornis*, *P. subreniformis* and *P. torrana*, there is no question that it is a distinct species and the information provided in this study should allow easy discrimination of the four species in future. It is still unknown whether any of these four occur sympatrically. Although *P. caucensis* and *P. torrana* occur relatively close together in SW Colombia, *P. caucensis* occurs on the eastern slope of the Cordillera Occidental of the Andes in the Department of Valle del Cauca and *P. torrana* occurs on the western or Pacific slope in the Department of Chocó (Fig. 7). It is somewhat more likely that *P. caucensis* occurs sympatrically with *P. bicornis*, which is more widely distributed, though *P. bicornis* has not been recorded in Valle del Cauca to date (Luer 1999, Tropicos 2017).

There has recently increased interest in the orchid flora of the Department of Valle del Cauca, Colombia (Kolanowska 2014, Kolanowska *et al.* 2011, Kolanowska & Szlachetko 2014, Reina-Rodríguez & Tupac-Otero 2011, Rodríguez-Martínez *et al.* 2015). However, the region is undoubtedly understudied and deserves further attention in order to fully describe the orchid flora before climate change and deforestation cause even more habitat loss (Reina-Rodríguez *et al.* 2016). The only known locality of the species described herein, *P. caucensis*, occurs in an unprotected area near Calima Lake where author Haelterman has observed other undescribed species of *Pleurothallis* in the nearby montane forest. A complete census of the orchid flora of this region could reveal multiple new species and further, provide support for forest protection in the future.

Relatively little is known about the pollination of species of *Pleurothallis sensu* Pridgeon *et al.* (2005), though most species are believed to be pollinated by

Diptera and a few by Coleoptera and Hymenoptera (Duque 1993, Calderón-Sáenz 2011, Duque-Buitrago *et al.* 2014). With regard to the role of labellar morphology in pollination in *Pleurothallis sensu* Pridgeon *et al.* (2005) even less is known (Dupree & Wilson 2016, Wilson *et al.* 2016). Other genera in subtribe Pleurothallidinae have been studied in much greater depth, including *Anathallis* (Cardoso-Gustavson 2014), *Dracula* (e.g. Policha *et al.* 2016), *Lepanthes* (Blanco & Barboza 2005), *Octomeria* (Cardoso-Gustavson 2014), *Restrepia* (Millner & Baldwin 2016), *Specklinia* (e.g. Karremans *et al.* 2015) and *Stelis* (Ignowski 2015, Ignowski *et al.* 2015). In some of these Pleurothallidinae a glenion is present on the hypochile of the lip which may act as a nectary-like tissue, producing a pollinator reward. In *Pleurothallis* the glenion is pronounced in subsections *Macrophyllae-Fasciculatae* (Wilson *et al.* 2016) and *Acroniae* (Wilson unpubl. data), but Luer (1999) stated that it is not usually developed in subsection *Macrophyllae-Racemosae* or *Antenniferae*.

Of the species studied here *P. bicornis*, *P. caucensis*, *P. subreniformis* and *P. torrana* all possess relatively simple lips. The flowers of *P. caucensis* appear to provide a liquid reward on the anterior margin of the central lobe of the labellum (Fig. 10), which is uppermost due to the apparently non-resupinate presentation of the flowers on the raceme (Fig. 1). While the glenion is not very distinct in *P. caucensis*, or the other species examined, at least compared to members of the *Macrophyllae-Fasciculatae* (Wilson *et al.* 2016), there does appear to be secretion of a liquid from under the anther which forms a layer between the two calli on the anterior edge of the lip (Fig. 11). We hypothesize that a potential pollinator lands on the synsepal and is attracted to the liquid reward on the anterior edge of the labellum and then proceeds toward the anther in response to the liquid reward accumulating between the calli on the lip. Most likely this model based on *P. caucensis* also applies to other members of the *Macrophyllae-Racemosae* with a simple lip, such as the *P. bicornis*, *P. subreniformis* and *P. torrana* studied here.

Conclusions. Considered together, *Pleurothallis* subsections *Macrophyllae-Racemosae* and *Antenniferae* comprise the second most species-rich group in the genus after subsection *Macrophyllae-*

Fasciculatae. Due to the difficulty in identification of members of this group, likely the species count is underestimated. Further, recent access to previously inaccessible areas of Colombia and northwestern Ecuador will likely reveal multiple new species. *Pleurothallis caucensis* described here is the first of a series of new species in the *Macrophyllae-Racemosae/Antenniferae* group. In addition to taxonomic studies, *in situ* research into the pollination ecology of the group would be highly desirable.

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